THE INNER EAR OF *GORGONOPS* (REPTILIA, THERAPSIDA, GORGONOPSIA)

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(With 6 figures)

I welcome the opportunity to express my admiration and thankfulness to Dr Boonstra, to whom the mammal-like reptiles and myself are greatly indebted.

It is to Watson that we owe the first tentatives toward elucidating the structure of the inner ear in mammal-like reptiles (cynodonts), but it was Olson (1944) who undertook a systematic study of this region of the skull in the main therapsid infra-orders. Olson's work included two gorgonopsians: the type of *Cyonosaurus longiceps*, and a form not generically identified, but which he considered as 'more primitive than *Cynariops robustus*,' the genus to which he had originally (1938*a*) assigned it. Thus it is only a modest supplement to his comparative study that is presented here. The genus *Gorgonops* would be situated, according to the conclusion I reached in 1970, at a higher evolutionary level than the two forms studied by Olson.

The method employed here to study the specimen of *Gorgonops* (B.P.I. 277) was that of serial sectioning, such as was used by Olson (1944) and previously by Romer & Price (1940) for the study of the inner ear of *Dimetrodon*. Details of the process I used (in reality not sectioning, but a grinding of the specimen) will be given later in a publication on the ensemble of the skull; it should be mentioned here that the latter measured about 237 mm long, and that grinding proceeded at ¼ mm intervals.

The preservation of the specimen turned out to be less satisfactory than was initially expected, and flattening of the posterior part of the skull is rather marked. The ear region is in reasonably good condition, but the defective ossification of this region renders its interpretation delicate and numerous uncertainties remain.

The inner ear is lodged, in *Gorgonops*, in the prootic, the opisthotic, the supraoccipital and the basioccipital. It is situated between sections 230 A—300 A.[1]

An immediately noteworthy fact concerns the inclination, dorsally and anteriorly, of the ear, this being in correlation with the same slope of the basicranial axis (Fig. 1). The mesial wall of the ear is only ossified at the back; there does not exist, therefore, on the endocranial face a proper internal auditive foramen, but a vast opening which leads into the cavity of the bony ear in which was contained the membranous ear. Obviously, the eighth cranial nerve

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[1] The section numbers cited in this work refer to the left side, but in fact there is very little offsetting from one side to the other.

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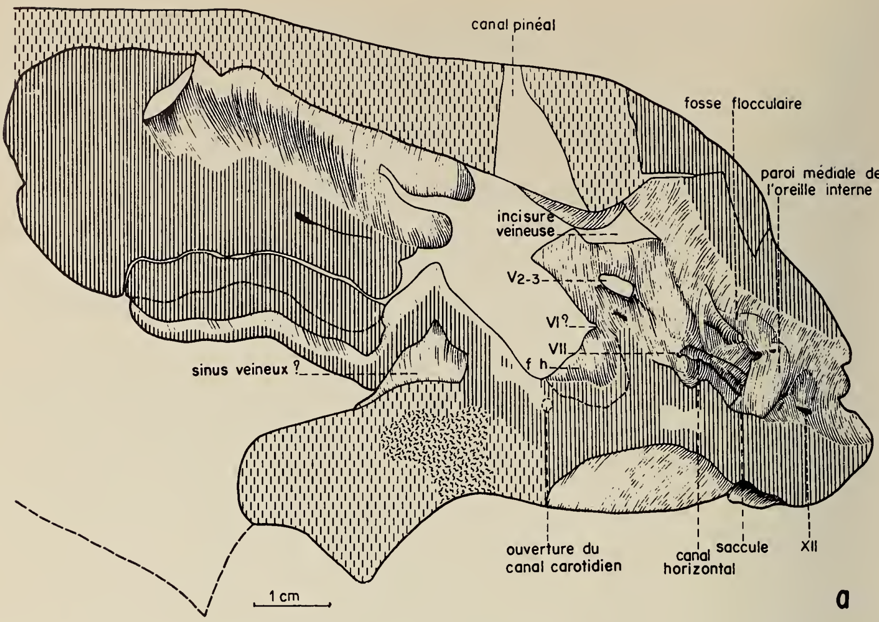

Fig. 1. Longitudinal section of the posterior part of the skull of *Gorgonops torvus* (B.P.I. 277), reconstructed from serial sections (from Sigogneau 1970). × 1.
f h: hypophyseal fossa.

also traversed this opening. The latter, in conjunction with the cavity of the bony ear, correspond to the vestibule of some authors, but it would be preferable, as noted by Romer (1955), to avoid this term originally applied to the upper part of the internal bony ear. The absence of ossification is such that the interior of the horizontal semicircular canal, contained in the lateral wall of the ear, is visible mesially; the canal, nearly totally lacking an internal wall, seems to open into the utriculo-saccular cavity. The same absence of ossification is responsible for the opening of the vertical anterior semicircular canal into the bony floccular fossa.

Indeed, intruding between the elements of the inner ear was an enormous flocculus (o),[2] directed postero-laterally after having passed anteriorly under the anterior semicircular canal. This flocculus must have been remarkably developed, and even partially covered the crus communis canalium. Opening anteriorly into the cerebral cavity, the floccular fossa penetrates first the prootic, which surrounds it on three sides; at the same time its floor, oblique ventrally and toward the median line, progressively rises until it becomes horizontal. But soon the supraoccipital invades both the roof and the floor, and when the fossa closes mesially (section 278 A), it is nearly completely included in the supraoccipital; it narrows progressively within this bone and terminates 1,5 mm behind its mesial closure.

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[2] This and following numbers refer to features in the figures.

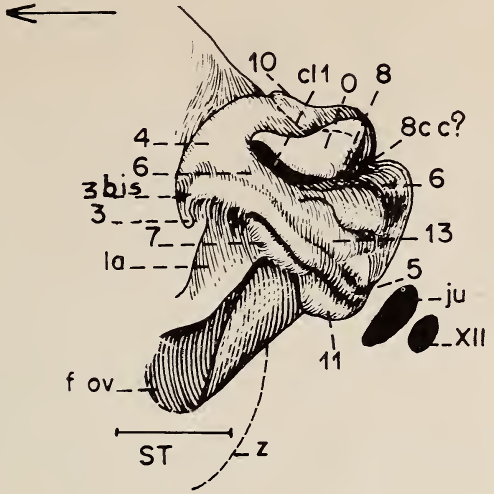
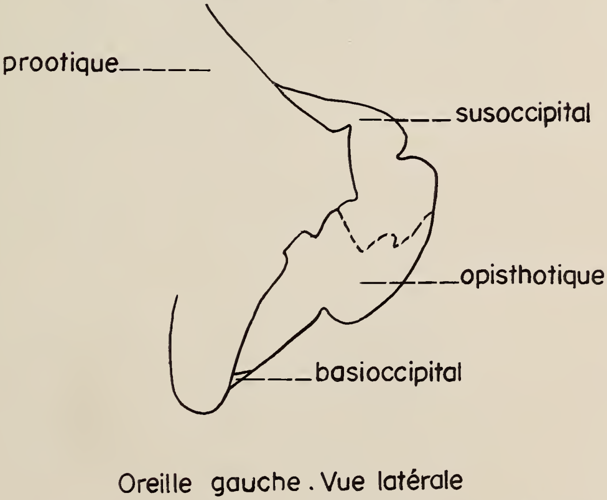


Fig. 2. Lateral view of the internal ear of *Gorgonops torvus* (B.P.I. 277), reconstructed from serial sections. × 2.
cl_1: emplacement of the partition between the floccular fossa and the ear proper; f ov: fenestra ovalis; ju: jugular foramen; la: lagenar recess; z: perilymphatic cistern?
o: floccular fossa; 3: anterior ampulla; 3 *bis*: external ampulla; 4 and 10: anterior vertical canal; 5: horizontal canal; 6: utriculus; 7: ventral part of the sacculus; 8: 8 cc: crus communis? 11: posterior ampulla; 13: dorsal part of the sacculus.
ST: antero- posterior extension of the stapes.



Oreille gauche . Vue latérale

Fig. 2 *bis*. The same as Figure 2, showing the emplacement of the sutures.

In the ear itself the three semicircular canals, the utriculus, the sacculus and the lagena were sought. The perilymphatic system certainly left traces, but they are difficult to identify.

The vertical anterior canal (4) is distinctly longer than the posterior canal; also, because of the inclination of the ear, the dorso-posterior slope of the canal is slight; it bends mesially to meet the vertical posterior canal. This anterior canal originates in a very short ampulla (probably the external ampulla) (3 *bis*), the latter being preceded by a small but deeper cavity inclined ventro-laterally (anterior ampulla) (3). Soon the ventral edges of the anterior canal approach each other (section 258 A), and it becomes enclosed within the thickness of the prootic, lateral to the floccular fossa. It rises progressively inside this bone, passes above the prootic partition which separates the floccular fossa from the internal ear, and attains thereby the roof of this fossa. When the supraoccipital invades this roof (*c*. 270 A), a curious phenomenon is observed: the orifice becomes double, with the lateral part (enclosed in the prootic) closing rapidly, and the mesial part (10) (situated first at the prootic-supraoccipital limit (Fig. 4, section 268 A), then in the supraoccipital alone) increasing in size and relaying the first canal; it then encircles the floccular fossa and mesially joins the posterior part of the ear. I originally saw, here, the replacement of the anterior canal by the posterior canal, especially since the situation is identical on both sides of the skull. But the utriculus is not visible at this level: we are above the floccular fossa in which the two canals open ventrally. An interpretation of this mesio-lateral doubling remains to be found; I have seen no example of it in the literature. For the present, I will consider that it is all the same anterior canal which continues until opening into the utriculus at section 285 A; this canal terminates 2 mm farther.

The posterior canal was much more difficult to identify. It is regarded here as being formed by the mesial half of the posterior otic cavity (Fig. 4, section 295 A), and is, in consequence, masked in lateral view by the other constituents of the latter; there would be no bony separation between the two. But Olson shows the posterior canal in the sections of '*Cynariops robustus*' (1938*a*, fig. 7, sections A and D) as being more lateral than the vertical anterior canal. I have found nothing equivalent; in any case, this canal must constitute the most posterior part of the ear; as a final argument, I will add that the structure here identified as the posterior canal terminates, as it should, in what is considered to be the posterior ampulla (11). This canal would be very short.

The horizontal canal (5), on the other hand, is easy to follow: it begins in the prootic in the same ampulla as the vertical anterior canal, and closely behind it (section 247 A). At first they are separated only by a fine crest, then after the definitive individualization of the latter, the horizontal canal penetrates laterally, slightly sloping downwards; its floor becomes formed by the opisthotic (section 272 A) and, one millimetre farther, the roof becomes formed by the supraoccipital. It continues, totally enclosed in the latter bone, as far as section 285 A, still sloping downward but bending mesially, and terminates in

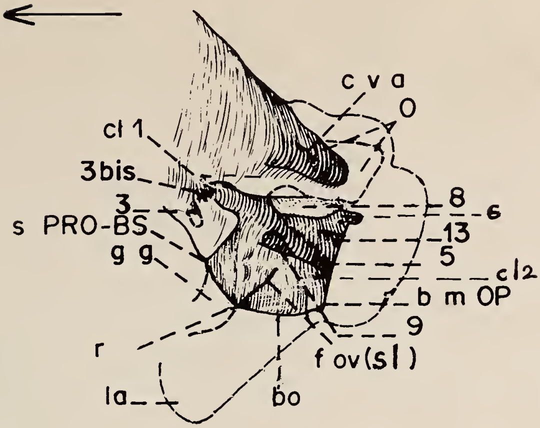


Fig. 3. Cavity of the internal ear of *Gorgonops torvus* (B.P.I. 277) seen in mesial view; reconstructed from serial sections. × 2.

b m OP: mesial border of the opisthotic closing the ear mesially; bo: mesial ossified border of the lagenar recess; cl_1: partition between the floccular fossa and the ear proper; cl_2: prootic then opisthotic partition closing cavity 9 mesially, and constituting the lateral wall of the lagenar recess; c v a: opening of the vertical anterior canal in the floccular fossa; g g: fossa situated under the cranial floor and corresponding perhaps to the geniculate ganglion; la: lagenar recess; r: level where the basioccipital replaces the basisphenoid as the dorsomesial border of the lagenar recess; s PRO-BS: separation of the basisphenoid and the prootic allowing the passage of the lagena above the cranial floor; sl: slit prolonging the fenestra ovalis.

o: floccular fossa; 3: anterior ampulla; 3 *bis*: external ampulla; 5: horizontal canal; 6: utriculus; 8: see text p. 58; 9: ventral part of the sacculus? 13: dorsal part of the sacculus.

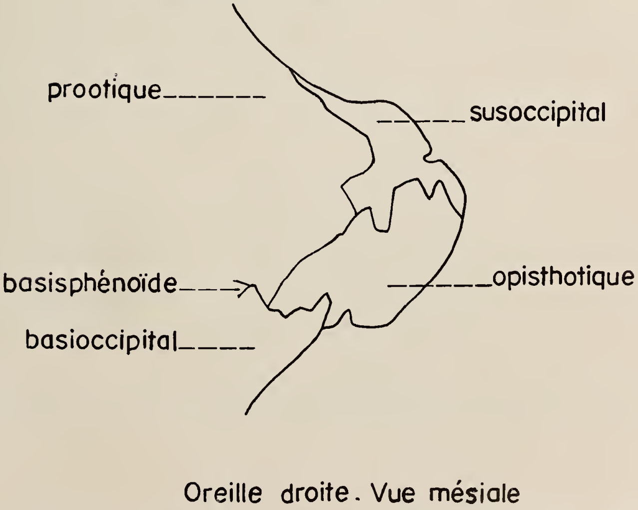


Fig. 3 *bis*. The same as Figure 3, showing the emplacement of the sutures.

the posterior ampulla just behind the opening of the sacculus. Taken in its entirety, the horizontal canal is, therefore, inclined postero-ventrally and scarcely rises again at the rear; it is rather convex laterally. Its mesial wall is more or less ossified according to the location, but never completely.

The ampullae are not as clearly recognizable as one would expect; this is particularly true for the anterior and external ampullae. The ear begins with a minute recess (1 mm by 2,5 mm) directed laterally and ventrally (Fig. 4a, section 240 A, 3); this should represent the anterior ampulla since it precedes the depression (1 mm by 1 mm) in which the anterior and horizontal canals originate and which should therefore be the external ampulla. The recess here interpreted as the posterior ampulla is, on the contrary, very well developed. In fact, its great antero-posterior extension created some doubt about this interpretation, and I at first thought it to be an element of the perilymphatic system. But its mesial situation, and especially its posterior connection with the horizontal canal, seemed to constitute convincing arguments in favour of the ampullar hypothesis; the vertical posterior canal then, would communicate with this ampulla dorsally and mesially with respect to the horizontal canal.

The crus communis canalium (8 cc), very mesially situated, starts also, in my interpretation, very posteriorly (section 282 A); it should open into the utriculus.

The central part of the ear presents a series of concavities which overlap each other latero-mesially. One of them (6) begins at the front of the ear and communicates there with the anterior and horizontal canals; it continues all the way to the posterior part of the ear where it receives, on its mesial side, the posterior canal; it should therefore represent at least the dorsal part of the utriculus. Ventrally this utriculus communicates first (Fig. 4a) with the lagena(la), then (Fig. 4b) with that which is interpreted here as the sacculus (9), and finally with the posterior ampulla, from which it is isolated farther on by the posterior canal. The utriculus terminates very posteriorly (at about section 295 A). It is doubled mesially by a cavity (8), of which we also have only the roof (the latter being at first constituted by the prootic, then by the supraoccipital) and from which it is separated by a crest. This cavity, the most mesial element of the ear, begins about section 260 A and also continues all the way to the rear. I could not identify it with certainty; it probably could not be the endolymphatic sac, which would thus be intraotic.

Between the utriculus and the horizontal canal is a cavity still better delimited dorsally (13) as well as ventrally (7) and more prominent than the preceding ones, but of smaller dimensions (approx. sections 260 A-290 A), and that I have regarded as corresponding to the sacculus. Its floor is in fact divided (7 and 9) for a great part of its length, but it is difficult to know if the two cavities are parts of the same element. The horizontal canal opens directly into this cavity, which, as noted above, communicates dorsally and mesially with the utriculus. Antero-ventrally the pocket opens into the lagena (Fig. 4a, section 260 A); when the latter closes, a crest rises from the opisthotic isolating the sacculus from the posterior ampulla (Fig. 4b, sections 268 A and 278 A). This so-called sacculus goes farther dorsally than ventrally. The interpretation given here for the sacculus is in opposition to that of Olson (1938*a*), where the saccular recess, indistinctly separable from the lagena, does not extend above the level of the horizontal canal, and to that of Romer & Price (1940), where the sacculus in *Dimetrodon* is situated below the level of the cranial floor. In this feature in *Gorgonops*, I had thought to recognize an element of the perilymphatic system, but it would be surprising that such an element would be so dorsal, that it would intergrade with the parts of the ear properly speaking,[3] and that it would be so distant from the fenestra ovalis.

Finally, the lagenar recess (la) constitutes an elongate tube sloping slightly antero-ventrally. Its anterior limit is difficult to determine (perhaps section 232 A), being situated in a very poorly ossified zone. The anterior part of the recess is lodged between the basisphenoid dorsally, the prootic dorso-laterally, and the basioccipital ventrally; then farther posteriorly (section 244 A), the opisthotic starts to form its lateral wall. Anteriorly, the lagenar recess is entirely below the level of the cranial floor. It opens laterally in a deep depression (Fig. 4a, z), the edge of which receives the stapes, and mesially in a small rounded recess interpreted as the receptacle for the geniculate ganglion (gg). When the prootic and basisphenoid separate, the dorsal part of the lagena passes above the level of the cranial floor, and soon (section 250 A) opens directly into the cerebral cavity. Only after the anterior third of the ear (section 260 A), and by the junction of the lateral and mesial parts of the opisthotic, is the lagenar recess completely closed laterally. It then narrows and terminates by a small circular fossa excavated in the opisthotic alone, in the floor of that which I have interpreted above as the posterior ampulla (Fig. 4*b*, section 268 A). In its middle part this recess communicates dorsally with the utriculus and mesially with the sacculus.

Concerning the perilymphatic system, three elements have been sought: the cistern, or reservoir of liquid at the level of the upper, or vestibular, part of the ear; the duct which prolongs the cistern and parallels the lagena particularly at the level of the basilar papilla (scala tympani); and finally the perilymphatic sac, the termination, in part at least extraotic, of the duct, lodged in what is improperly called the recessus scalae tympani.

On this subject a parenthetical explanation is perhaps not superfluous. In tetrapods, and with the appearance of the fenestra ovalis, the perilymphatic space which isolated, in fishes, the membranous ear from the bony ear becomes organized into a specialized system for the conduction of vibrations from the outside environment to the properly sensorial zone of the membranous ear, the basilar papilla of the lagena. This system is composed of, first of all, a

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[3] However Romer & Price write (1940) with respect to *Dimetrodon:* 'Cavities which are apparently associated with the perilymph system push outwards within the loops of the two vertical canals. . . .'

230 A 240 A

250 A Fig. 4a 260 A

Fig. 4a. See legend opposite page.

roughly circular cavity, the perilymphatic cistern, applied to the lateral opening that is the fenestra ovalis,[4] and therefore against the stapes. From this cistern

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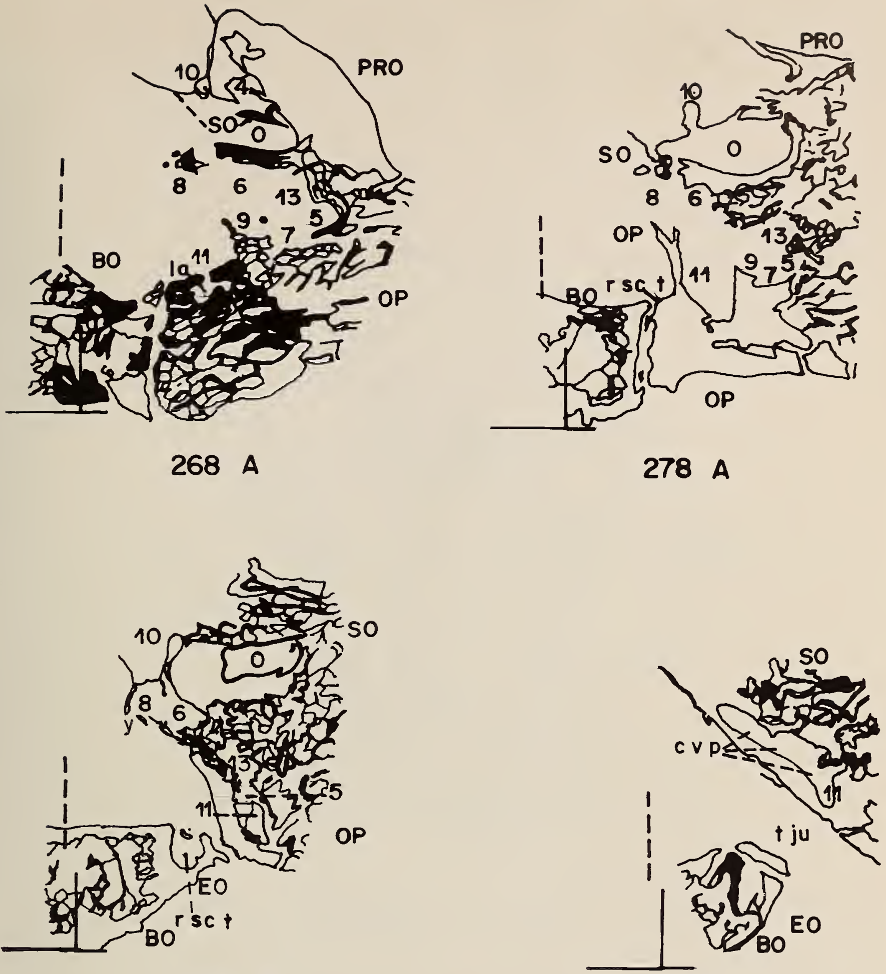
[4] Or foramen vestibuli, called thus because it is situated at the level of the vestibule of the ear. This is not true, however, in certain living reptiles, nor in the mammal-like reptiles, where it opens at the level of the lagena.


268 A

278 A

285 A

295 A

Fig. 4b

Fig. 4. Some of the serial sections of the ear region of *Gorgonops torvus* (B.P.I. 277). × 2. a) anterior part of the ear; b) posterior part.

c v p: posterior vertical canal; f ov: fenestra ovalis; g g: fossa corresponding perhaps to the geniculate ganglion; la: lagenar recess; r sc t: recessus scalae tympani? t ju: jugular canal; y: foramen corresponding perhaps to the endolymphatic duct; z: perilymphatic cistern?

o: floccular fossa; 2: fossa from which the ampullae will develop; 4 and 10: anterior vertical canal; 5: horizontal canal; 6: utriculus; 7 and 9: ventral part of the sacculus; 11: posterior ampulla; 13: dorsal part of the sacculus.

BO: basioccipital; BS: basisphenoid; PRO: prootic; OP: opisthotic; SO: supraoccipital; ST: emplacement of the stapes.

The sutures have been omitted in the interest of clarity, although they are discernible in the sections.

The dotted line corresponds to the median axis of the cerebral cavity.

a tube leaves, the perilymphatic duct; in lower tetrapods the latter is applied against the basilar papilla for part of its length by the intermediary of the basilar membrane. Beyond this papilla it attains the lower posterior bony wall of the otic capsule, a wall that it traverses by the perilymphatic foramen (called in error by some authors the fenestra cochleae). From there it spreads out into another evagination, the perilymphatic sac. The latter, apart from its dorsal opening into the duct, opens mesially into the cerebral cavity (by an internal jugular foramen, so-called because it is utilized at the same time by the jugular or posterior cerebral vein) and extends into the subarachnoid lacunae. Laterally, it comes in contact with the tympanic cavity, where an opening pierces the wall of the otic capsule, the fenestra rotunda sensu lato, or pseudo-fenestra rotunda. Thus, not only are the vibrations transmitted by the stapes received by the perilymphatic liquid, which fills all of the system described, and conducted to the level of the basilar papilla where the sensorial cells receive the excitation, but the lower part of the system has, in addition, a compensating role necessitated by the incompressibility of liquids; thus a mesiad depressing of the tympanum results in a laterad depressing of the secondary tympanic membrane, which obstructs this pseudo-fenestra rotunda.

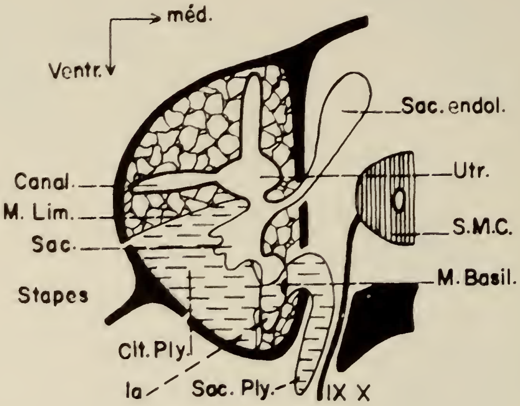


Fig. 5. Interrelationship of the peri- and endolymphatic systems in *Sphenodon* (from De Burlet).

On this scheme a certain number of variations are realized. It is necessary, if not logical, to begin with mammals, because it is with them that the terms were first defined. In this class, then, the lagena has acquired such a length that it coiled up in a cochlea. The perilymphatic sac has become intraotic, and it is this structure (not the perilymphatic duct) that is applied against the basilar membrane. This perilymphatic sac has followed the coiling of the cochlea (or scala media) along each side, forming thereby a double tube: one part, the vestibular ramp, or scala vestibuli, is directly connected to the fenestra ovalis; the other part, terminating at the secondary tympanic membrane (closing the fenestra rotunda sensu stricto), is the tympanic ramp or scala tympani. It follows, therefore, that, according to this definition, it is the scala tympani which is applied against the basilar papilla (in mammals called the organ of Corti).[5]

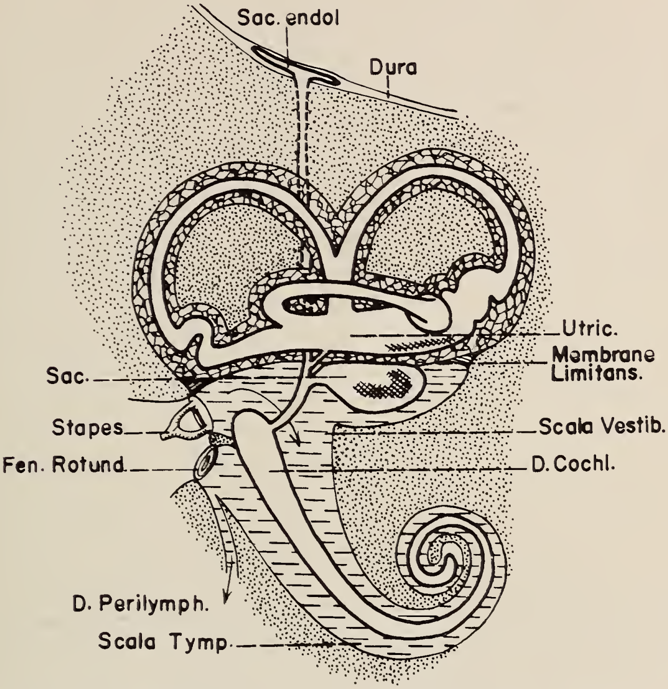


Fig. 6. Interrelationships of the peri- and endolymphatic systems in mammals (from De Burlet).

By homology, the part of the perilymphatic system which in reptiles forms the same support for the basilar papilla is also called the scala tympani,[6] even though it concerns the perilymphatic duct, and not, as in mammals, the perilymphatic sac. This difference leads to a dislocation of the terms: the bony cavity which in mammals encloses the scala tympani (that is, the whole perilymphatic sac) constitutes the recessus scalae tympani. By homology, but a somewhat perverse homology, the (incomplete) bony cavity which houses the

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[5] It should be noted that, despite this development, the internal ear is entirely included in the periotic; this is also the case in living reptiles, but in mammal-like reptiles, as was seen above, not only the periotic but also the basioccipital participates in the bony internal ear. In cynodonts, however, this bone is reduced to a minimal participation.

[6] This term is all the more improper in that the lagena is here short and straight, and that the duct is not parallel, but perpendicular to it; there are not, therefore, two ramps. In crocodiles the lagena is elongate and the ramps are discernible, but they remain straight.

perilymphatic sac in reptiles has received the name of recessus scalae tympani, even though, let it be repeated, the scala tympani is here constituted by the duct and not by the perilymphatic sac, and is not, in consequence, contained in the 'recessus scalae tympani'. Moreover, this recessus is in reptiles an extraotic and extracerebral space (enclosed either between the periotic and the supraoccipital, or within the exoccipital). Its embryological origin goes back to the metotic fissure, that is, the space left between the embryonic otic capsule and the base of the skull. This fissure, in the embryo, serves not only as an opening for the perilymphatic sac, but it forms also a passage for the cranial nerves IX, X, XI, and the jugular vein.[7] In mammals (as well as in crocodiles and in birds, although by a different process) the recessus has become entirely closed and intraotic by the secondary formation of a bony floor. In the course of this process the openings have been preserved, but at the same time submitted to modifications which result in, for example, the lateral opening (or fenestra rotunda) not being entirely homologous to the opening of the same name in reptiles.

Many other homologies have been proposed. I have lightly touched upon the problem here, only wanting to explain the terms utilized.

To come back to *Gorgonops*, this cistern is probably indiscernible at the level of the fenestra ovalis, unless, ventrally and laterally to the lagenar recess, a non-ossified region between the basioccipital and the prootic (sections 230 A–246 A) represents a trace of this cistern (Fig. 4a, z). The perilymphatic duct also remains indistinct, although a part of the cavity interpreted as the posterior ampulla may correspond to it. On the contrary, it has been thought possible to detect a trace of the perilymphatic sac in the form of a 'recessus scalae tympani': there exists (Fig. 4b, section 278 A), on the mesial side of the opisthotic partition closing the ear posteriorly, a depression which opens farther to the rear (section 284 A) into the jugular passage; the latter must therefore represent the whole of the metotic fissure (the jugular foramen plus the pseudo-fenestra rotunda).

Finally, concerning the endolymphatic sac, I have evoked the possibility that the depression (discernible in the prootic, then supraoccipital, partition) which separates the floccular fossa from the ear proper (8) could represent the trace of this sac. Another possibility is that the orifice which persists posteriorly (Fig. 4b, section 285 A, y), in the mesial wall of the bony ear, corresponds to the passage of the endolymphatic duct towards this sac, which would be, in that case, more mesial.

The fenestra ovalis is situated very anteriorly; moreover, it does not open at the base of the lagenar recess, but ventro-laterally with respect to it (Fig. 2). One can, therefore, consider that it has started to rise towards the vestibular part of the ear, where it lies in living reptiles and mammals, and where it is properly a 'fenestra vestibuli'. Furthermore, whereas in these two cases it pierces the otic capsule, it is here included between the otic capsule and the

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[7] In the adult, different cases are possible: the recessus scalae tympani can fuse with the jugular canal; it can also contain only the perilymphatic sac and the nerve IX.

base of the skull. Olson had already noted this last point in 1938, but the fenestra ovalis and the metotic fissure are, in *Gorgonops*, independent of each other. The anterior edge of the fenestra ovalis is no more distinct than that of the lagenar recess. Anteriorly it is bounded dorsally by the prootic, ventrally by the basioccipital. It almost closes (section 248 A) by the intervention of the mesial part of the opisthotic, but it is prolonged by a slit (2,5 mm long) as far as the complete junction of this mesial part with the lateral part of the bone, which results in the disappearance of the prootic from its roof (section 261 A). Behind its closure persists, in the opisthotic, a conical depression one millimetre long. The stapes covers all of the fenestra ovalis, and half of the slit. One might suppose that the two millimetres remaining behind the stapes (half of the slit plus the posterior fossa) were occupied by a cartilaginous expansion.

That which has been very tentatively interpreted here as the mesial orifice of the nerve VII is situated slightly in front of the level of the horizontal canal; the nerve would then cross the bone, somewhat obliquely towards the front and laterally, and would exit just in front of the ear (Fig. 1). The position of the geniculate ganglion would be visible ventrally and behind nerve VII, between the prootic and the basisphenoid (Fig. 4a, section 240 A, g g).

The nerves IX, X and XI must have exited by the jugular canal, which passes first between the opisthotic and the exoccipital then, farther toward the rear, inside the exoccipital (Fig. 4b, section 295 A); this canal is completely separated from the posterior part of the ear by a bony wall.

Comparison with other Gorgonopsians

As has been noted above, the internal ear has already been studied in *Cyonosaurus longiceps* (*Cistecephalus* zone[8]) by Olson in 1937, and the same author in the following year sectioned a skull of '*Cynariops*' (*Endothiodon* zone[8]) and reconstructed the membranous labyrinth. In 1944 he made several modifications in his reconstructions. The comparison of these with that proposed here for *Gorgonops torvus* (*Endothiodon* zone[8]) may indicate a certain evolution of this region within the gorgonopsians.[9]

In all three cases a feeble degree of mesial ossification can be observed. The separation of the floccular fossa from the internal ear proper intervenes in the three cases also, but the partition is here parallel to the horizontal canal, whereas it forms with the latter an angle of about 65° in *Cyonosaurus* and 45° in '*Cynariops*'. One would witness here, if the proposed morphologic sequence is accepted, a dorsal migration of the floccular fossa, which, from an anterior position, would become dorsal.

The floccular fossa seems to have approximately the same depth in the three forms. Also it is partially enclosed in the supraoccipital.

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[8] *Sensu* Broom.

[9] In a previous study (1970), I considered that *Cyonosaurus* was the most primitive gorgonopsid, that *Gorgonops* would be a rather evolved form, and that '*Cynariops*' would be situated morphologically between the two.

The anterior semicircular canal is always longer than the posterior, but the difference in length is greater in *Gorgonops* and in '*Cynariops*' than in *Cyonosaurus*. As for the individualization of the posterior canal from the crus communis, it is the least marked in *Gorgonops*. The horizontal canal would be more convex here than in the genera studied by Olson, a fact which, according to him, would constitute a primitive character.

The anterior and external ampullae seem to have been well individualized, in *Cyonosaurus* at least; the external ampulla is not figured in '*Cynariops*', and the difficulty met with in distinguishing both of them in *Gorgonops* has already been commented on; they seem to have been, in any case, smaller here.

The comparison becomes more difficult for the utriculo-saccular region, due to the fact that my interpretation differs from that of Olson. The latter considered that the sacculus was entirely situated in the lower part of the ear, indistinct from the lagena, with the ensemble forming what he calls the sacculo-cochlear recess. I have, on the contrary, suggested that the cavity, above and below the horizontal canal and mesial to it, could hardly represent anything but the sacculus, whereas the crus communis and the utriculus would be less well individualized. A side by side comparison of the material is needed to resolve this matter.

The lagenar recess is even longer here than in *Cyonosaurus*; it was very short in '*Cynariops*'. It is very mesially situated in *Gorgonops* and oriented ventro-anteriorly, whereas it is directed towards the rear in *Cyonosaurus* and becomes vertical in '*Cynariops*' and a little more anterior than in the preceding genus. One can therefore confirm the tendency noted by Olson, wherein the lagena would migrate anteriorly and mesially in an evolutionary sequence. *Gorgonops* would then be situated above the two others in this regard.

The fenestra ovalis, instead of being, as it is here, antero-lateral with respect to the lagena, is definitely ventral in the two genera studied by Olson, and even oriented a little posteriorly in *Cyonosaurus*. This situation, like that of the lagena, makes of the ear of *Gorgonops* an evolved structure with respect to that of the two preceding genera.

But, on the contrary, the supposed position of the orifice for nerve VII, slightly in front of the horizontal canal, does not prolong the sequence sketched according to Olson by the two other gorgonopsians; in his view this orifice should migrate toward the rear in an evolved form. This point will be taken up further on.

As in *Cyonosaurus* and '*Cynariops*', the jugular foramen is isolated from the internal ear by a bony wall, although this foramen is less posteriorly situated here.

In 1938 Olson indicated the trace in '*Cynariops*' of an endolymphatic duct, leading to an endolymphatic sac situated against the suture separating the prootic and the supraoccipital, behind the floccular fossa. But in 1944 he interpreted this opening as the 'dorsal entrance of the sinus utricularis into the periotic' and as indicating 'the level of the junction of the utriculus with the crus communis canalium'. Whatever may be the interpretation of this structure, it seems that it agrees with that cited above in the mesial wall of the ear of *Gorgonops*.[10]

From this short comparison it can be seen, first of all, that the region of the internal ear shows a definite homogeneity in the three gorgonopsians discussed. But one can also discern indications of variability, even though it is difficult to decide in which direction the evolution occurred. To determine this, it would be necessary to methodically explore the infra-order. Neither does one know if this evolution was harbinging that was undergone by the more evolved theriodonts in their tentatives toward mammalness, or if, like the prootic bone, the ear of Gorgonopsidae evolved more or less against the trends seen in the other theriodonts.

On this topic, and in conclusion, some of the evolutionary tendencies presented by the therapsid internal ear can be envisaged. These were essentially brought out by Olson (1944).

According to this author, the relationship of the ear length to the length of the skull diminishes when the latter increases in absolute value. The specimen of *Gorgonops*, larger than all the theriodonts described by Olson, fully confirms this point of view, with a proportion of 0,06, which is lower than all the indices obtained by him. The relationship of ear width over length is very 'gorgonopsian' with 0,06, but it does not appear possible to follow a progression throughout the therapsid series. On the other hand, the height of the ear would make this specimen the most evolved of all, with 0,1 (the cynodonts, however, could not be evaluated in this respect).

The feeble degree of mesial ossification seems general, from the pelycosaurs to the cynodonts, with no sign of progress even in the latter. In most of the forms also, the anterior vertical canal apparently opens, by the same lack of ossification, into the floccular fossa. Finally, and paradoxically, it is only in *Dimetrodon* and the gorgonopsians that the jugular canal is separated by a bony wall from the labyrinthic cavity.

If the floccular fossa was shallow in pelycosaurs and the first anomodonts, it is, however, difficult to discern a precise evolutionary direction of this structure in the therapsid series, and still less to recognize a relationship between the fossa and the flocculus. One can say that it is in the three gorgonopsians, the therocephalian B of Olson, and in the cynodonts (Olson and Simpson), that the fossa is the deepest. On another point it seems to me that one can follow the migration of the flocculus from in front of the internal auditive foramen (anomodonts, gorgonopsians A and B of Olson), toward the dorsal side (*Pristerodon*, *Gorgonops*, therocephalians and cynodonts), and then toward the rear (mammals). But *Dimetrodon* adds a disturbing element to this sequence with a flocculus placed above the internal ear.[11]

According to Olson, the inequality between the anterior and the posterior

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[10] And with that noted by Simpson (1933) above and behind the floccular fossa in a cynodont.

[11] This constant reference to the specialized form that is *Dimetrodon* is hardly justified, except that it constitutes the only source of information we have for the pelycosaurian ear.

vertical canals increases as one rises stratigraphically through the anomodontid series. This is not valid in the gorgonopsids, since, by this trait also, *Gorgonops* differs from the other forms and attains the degree reached by the more advanced and later theriodonts. On the other hand, the canals are generally more distinct from the crus communis than they are here.

The lagena is contained in the prootic dorsally and in the basioccipital ventrally, an arrangement that began with *Captorhinus*. But the participation of the basioccipital diminishes progressively (cynodonts) as the ear rises in the periotic to attain a mammalian position. In this regard, *Gorgonops* occupies a primitive position; on the contrary, the migration of this structure anteriorly is as advanced in this genus as it is in the known cynodonts, and the mesial migration is even more marked. The fenestra ovalis would have followed the migration of the lagena.

As expressed by Olson, one could expect that the orifice of nerve VII would migrate toward the rear progressively with the increase in the general degree of mammalness. Unhappily, the available facts hardly confirm this supposition, since Olson's gorgonopsians A and B are in this respect 'evolved', and *Gorgonops* and the cynodonts lag behind.

It is supposed that the nerves IX, X and XI exited through the jugular canal in all forms. Let us keep in mind that this canal is isolated from the ear only in pelycosaurs, gorgonopsians and the cynodont studied by Simpson. The dicynodont ear described by Cox (1962) agrees, on the contrary, with the more general condition.

The nerve XII leaves by a single orifice in pelycosaurs, anomodonts, and gorgonopsians, and by two orifices in cotylosaurs, certain therocephalians and cynodonts.

In summary, defining a primitive stage for the therapsid ear as well as a general evolutionary direction is hardly easier than it is for the gorgonopsians alone. It is probable that each infra-order tried the ascension independently, by beginning at nearly the same low level. But there exists an obvious necessity to considerably extend our knowledge of each of these infra-orders before we can validly appreciate their positions with respect to each other, even as concerns only the internal ear region. This is all the more desirable since the latter is a very stable region, unaffected by secondary adaptations, and which, in consequence, should contribute to our understanding of the acquisition of the mammalian stage.

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